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THE ENERGY METABOLISM OF THE RAVEN CORVUS CORAX, (U)
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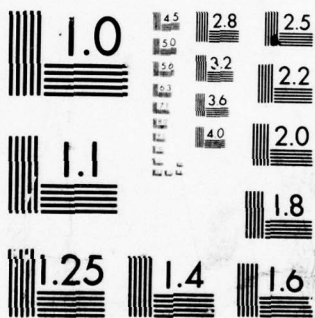
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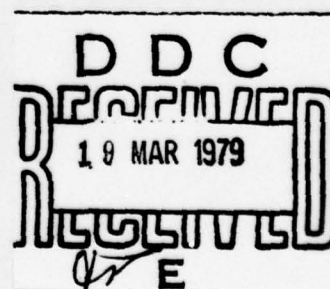
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THE ENERGY METABOLISM OF THE RAVEN CORVUS CORAX CORAX

by

V. R. Dol'nik



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Block	Italic	Transliteration	Block	Italic	Transliteration
А а	<i>А а</i>	A, a	Р р	<i>Р р</i>	R, r
Б б	<i>Б б</i>	B, b	С с	<i>С с</i>	S, s
В в	<i>В в</i>	V, v	Т т	<i>Т т</i>	T, t
Г г	<i>Г г</i>	G, g	У у	<i>У у</i>	U, u
Д д	<i>Д д</i>	D, d	Ф ф	<i>Ф ф</i>	F, f
Е е	<i>Е е</i>	Ye, ye; E, e*	Х х	<i>Х х</i>	Kh, kh
Ж ж	<i>Ж ж</i>	Zh, zh	Ц ц	<i>Ц ц</i>	Ts, ts
З э	<i>З э</i>	Z, z	Ч ч	<i>Ч ч</i>	Ch, ch
И и	<i>И и</i>	I, i	Ш ш	<i>Ш ш</i>	Sh, sh
Й й	<i>Й й</i>	Y, y	Щ щ	<i>Щ щ</i>	Shch, shch
К к	<i>К к</i>	K, k	Ъ ъ	<i>Ъ ъ</i>	"
Л л	<i>Л л</i>	L, l	Ы ы	<i>Ы ы</i>	Y, y
М м	<i>М м</i>	M, m	Ь ь	<i>Ь ь</i>	'
Н н	<i>Н н</i>	N, n	Э э	<i>Э э</i>	E, e
О о	<i>О о</i>	O, o	Ю ю	<i>Ю ю</i>	Yu, yu
П п	<i>П п</i>	P, p	Я я	<i>Я я</i>	Ya, ya

*ye initially, after vowels, and after Ъ, Ь; e elsewhere.
When written as ë in Russian, transliterate as yë or ë.

RUSSIAN AND ENGLISH TRIGONOMETRIC FUNCTIONS

Russian	English	Russian	English	Russian	English
sin	sin	sh	sinh	arc sh	sinh ⁻¹
cos	cos	ch	cosh	arc ch	cosh ⁻¹
tg	tan	th	tanh	arc th	tanh ⁻¹
ctg	cot	cth	coth	arc cth	coth ⁻¹
sec	sec	sch	sech	arc sch	sech ⁻¹
cosec	csc	csch	csch	arc csch	csch ⁻¹

Russian	English
rot	curl
lg	log

SUBJECT CODE 60

THE ENERGY METABOLISM OF THE RAVEN *Corvus corax corax*.

V. R. Dol'nik.

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Is studied dependence on the temperature of the medium of several indices of energy metabolism of the raven *Corvus corax corax* in winter period. Standard metabolism is equal to 120 kcal/day. At the low temperatures in rest, it composes 138.2-3.4 T_A kcal/day. Thermoneutral zone stretches from 6 to 36°C and is provided by three methods of the physical thermostatic control: by a change in the position of feathers(it provides 16° zones), with increase in the temperature of body (4°) and with respiratory evaporation (10°). The effectiveness of respiratory evaporation so is great, which makes it possible to preserve heat balance even at an air temperature of 50°. Energy of existence is equal to 176.6-1.1 T_A kcal/day.

Are examined the reasons for disagreements in the results of

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measurements, made by the different authors. Was compared metabolism of the raven with the metabolism of a passerine bird of the same weight, calculated by the generalizing formulas.

An analysis of the formulas of dependence on the size/dimensions of body and temperature of the medium of such indicators of metabolism as rest energy and energy of existence, is led to the conclusion that the upper limit of the size/dimensions of passerine birds is limited by weight approximately 0.5 kg (Kendeigh, 1970, 1972). In the sparrows of larger weight, must appear heat-regulating problems at the high temperatures of medium, thermoneutral zone must begin at the temperatures lower than zero, and upper boundary of thermoneutrality and superheating/overheating - at the moderate temperatures. Actually, the weight of the majority of large passerine birds, including Corvidae, is limited by 600 g. Only for ravens is it higher - it reaches at *C. c. corax* 0.8-1.4 kg, and of *C. c. tibetanus* - even 2 kg.

Usually animal-giants avoid superheating/overheating with the aid of special adaptations (denudation of the sections of body, bright stain/staining, narrow adaptation to inhabiting in the high latitudes or mountains). As is known, ravens extend from the arctic to the arid zones of Asia and Africa. *C. c. ruficollis* (weight 600 g)

dwells in Arabia at the day temperatures of approximately 40° (in the middle of day 50°). Black stain/staining under such conditions must contribute to superheating/overheating. The weight of plumage in it composes 80/o of the weight of body (Turcek, 1966) instead of 50/o, characteristic for the birds of this weight (Kendeigh, 1970). One special feature/peculiarity of the behavior of ravens indicates the frequent superheating/overheating. These are the only passerine birds, that fly usually with the open beak. Ravens very frequently sit with the open beak and open/disclose it in the moderate work. In hot moist weather it is possible to see, as from beak drips water.

In spite of exceptional interest in the energetics of passerines, it has been only slightly investigated, and results are contradictory. Thus, L. Irving (Irving et al., 1955) did not reveal/detect an increase in metabolic rate during a decrease in the temperature of the medium right down to 0° in experience/experiments on *C. caurinus*. On the contrary, J. West (West, 1965) found that the speed of metabolism in rest of *C. brachyrhynchus* grow/rises linearly from 30 to -30°, not forming thermoneutral zone. S. C. Kendeigh (Kendeigh, 1972) gives unpublished data of J. Harder, according to which in *C. c. rugicollis*, thermoneutral zone very narrow (from 30 to 38°) and standard metabolism is low.

V. M. Gavrilov (1973) measured the metabolism of several form/species of Corvidae, including of two subspecies of ravens - *C. c. corax* and *C. c. ruficollis*. Lower boundary of thermoneutrality of the first subspecies was at the level 6° , and of the second - 8° . Metabolism in rest at 0° of the first subspecies composed 147 kcal/day, and in thermoneutral zone - 127 kcal/day.

These contradictions impelled us to conduct the measurements of the metabolism of ravens, after paying special attention to thermoneutral zone.

MATERIAL AND METHODOLOGY OF STUDY.

For experience/experiments were used three tame ravens of the subspecies *C. c. corax*, which were being contained in winter in street volary at temperatures from 0 to -20° . The average weight of birds during experience/experiments was 1185 g. All the measurements are produced in the middle of night. Forage they removed for 6 h and more prior to the beginning of experience/experiment. For maintaining constant temperatures, was used the chamber for testing the

specimen/samples "Groenland" with the range of operating temperatures from -30 to +100° and the accuracy of thermostating 1°.

For research on the oxygen intake of birds, they placed into the hyaline/transparent airtight chambers with a volume of 19 L, equipped with electrothermometers. Duration of each measurement 20-30 min. Birds were located in the darkness. In certain cases after completion of measurement in the chamber, was included the gleam, making it possible through inspection window to see the pose of bird. The data on oxygen intake are recounted in kilocalorie from the relationship: 1 L of oxygen is equivalent to 4.8 kcal.

The temperature of body was measured remotely in other experience/experiments with the aid of the thermistor, introduced from evening 2 cm into the cloaca. The bird was located in the thermostatic chamber during the entire night. After a change in the temperature in thermostat, the measurement began after 15-30 min.

The respiratory (and skin) losses of water were determined in the flowing chamber through which the pump blew through the dried air. The outgoing airflow penetrated the vessel with the absorber of the water vapors, a change in weight of which (with correction for a change in the weight of the control vessel, through which it passed the air, which entered from the identical chamber without bird) it

served as the indicator of the liberation/excretion of water. Calculated atmospheric humidity in the chamber of approximately 30o/o. With the conversion of the losses of water to a quantity of spent to its evaporation energy, it is accepted that for evaporation 1 m² of water it is required by 0.58 kcal.

Energy of existence was measured according to the consumption of standard according to food nourishment value (nonfatty horsemeat) in experience/experiments the duration of 10 days each.

RESULTS OF STUDIES AND THEIR CONSIDERATION.

Oxygen intake by crows linearly grow/rose during a temperature decrease of medium from +22 to -19° (see figure). The level of oxygen intake was constant and lowest in the range from 22 to 36°. This standard minimum speed of metabolism of ravens is equal to 120 ± 0.11 kcal/day. By the formula of Lasiewski-Dawson (Lasiewski, Dawson, 1967) the passerine birds with a weight of 1185 g must have higher level of standard metabolism (145.9 kcal/day). Upper boundary of thermoneutral zone was at 36°, i.e., it is not lower than in the majority of passerine birds of smaller size/dimensions (King, Farner, 1961). In the range of temperatures from 36 to 40°, metabolism

sharply grow/rose, but at 40-50° this process it slowed down. Birds maintained a stay at 50°, at least, during 60 min.

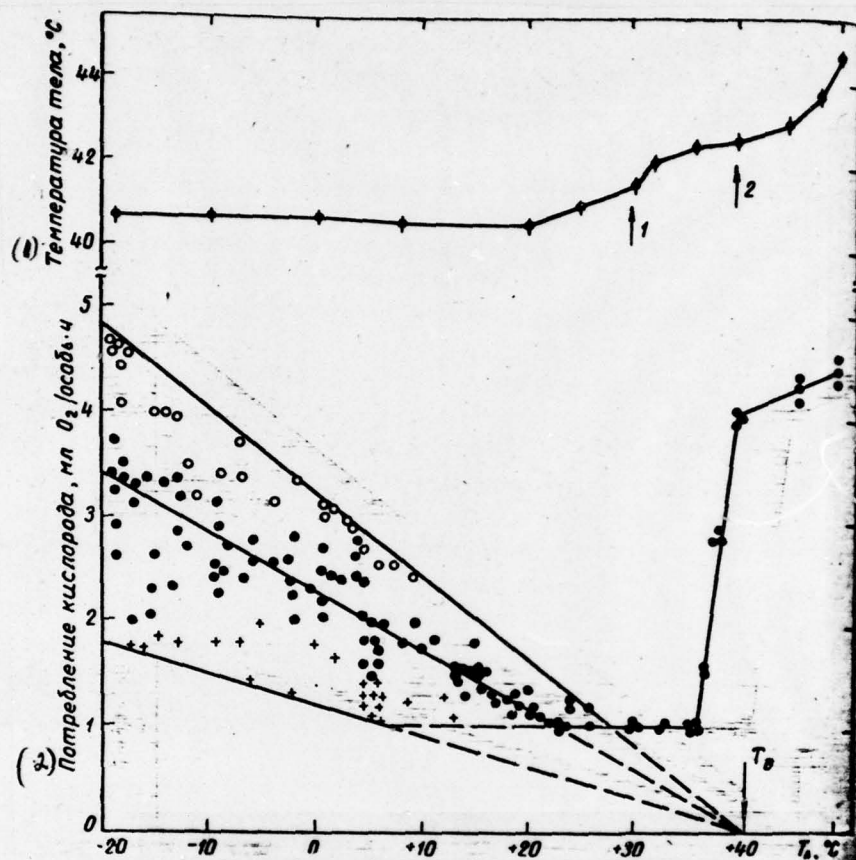
At the temperatures below 22° variation in the oxygen intake in various measurements grew with a temperature decrease. This is found in sharp contrast with the stability of metabolism at temperatures above 22°. In order to explain the reason for the oscillation/vibrations of oxygen intake when the obtained values were very low or very high, right after the end of experience/experiment in the chamber, was switched on illumination and noted the pose of bird. Ravens, like other passerine birds, have two poses of the sleep: one - with ruffled feathers, head "is pulled into shoulders", another with the pressed plumage.

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It turned out that the low oxygen intake was combined with the first pose, and high from the second. Under conditions of experiment, with the noise of the fans of the compressors and vibration of installation, ravens frequently change the poses, since the manifestation of excitation in them is connected with the pressing of plumage. Under calm conditions, in volary in the cold, to them during entire night is peculiar the first pose. At temperatures above 20°, on the contrary, bird always sit with the pressed plumage. The effect

of the position of plumage on the rate of oxygen intake is shown on several form/species of small birds, but only for a raven is the effect of pose so great.

Graphic construction of the dependence of the velocity of metabolism in rest on the temperature of medium to customarily perform on the basis of Newton's rule in the interpretation, given by Scholander for warm-blooded animals. According to this model, the metabolism grow/rises linearly with a temperature drop of medium lower than boundary of thermoneutrality; the extrapolation of line to the side of high temperatures must leave into the point of intersection of the speed of metabolism, equal to zero, with the temperature of medium, equal to the temperature of body.



The dependence of body temperature and oxygen intake on the temperature of the environment for ravens: o, + - the oxygen intake of oxygen by crows in pose with the pressed and ruffled feathers; • pose it is not determined; 1 polypous onset; 2 - onset of thermal dyspnea.

Key: (1). Temperature of body, °C. (2). Oxygen intake, ml

$O_2/\text{individual} \cdot h.$

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Calculated by the method of least squares regression on all our measurements at temperatures below 24° takes the form:

$$M = 260,0 - 6,39 T_A, T_A = T_B \text{ with } M = 0. \quad (1)$$

Here M - the speed of metabolism, kcal/day; T_A the temperature of medium; T_B the temperature of body (40.7°). Thermoneutrality in that case begins from 22° .

On the other hand, the line, drawn through lowest values of oxygen intake on section from lowest temperature (-19°) to the first measurement when oxygen intake was equal to standard level (6°) with extrapolation it gives $M = 0$ when $T_A = T_B$. It is possible to count that this - the boundary of the lowest level of metabolism during the complete utilization of an effect of pose with ruffled feathers and that is precisely such the metabolism in the latent in calm circumstances birds. Regression for this pose

$$M = 138,2 - 3,40 T_A. \quad (2)$$

while thermoneutrality begins from 6°. These values correspond to the results, obtained by V. M. Gavrilov (1973).

If we conduct the line, which restricts the highest points, then it also intersects abscissa at the point, which corresponds to the temperature of body. In this case the dependence is expressed by abrupt/steep line up to 30°, i.e., in all range of the measurements, carried out by West. This dependence corresponds to the metabolism of the excited or alerted birds. If J. West's and J. Harder's ravens were not tame, then the findings on the absence of thermoneutral zone up to 30° and abrupt/steep of increase of metabolism during a decrease in the temperature can be explained by excited state of these very cautious and "intellectual" birds.

The temperature of body of ravens in the range of the temperatures of medium from -30 to +20° is constant (40.7°). At higher temperatures it grows/rises, reaching at +50° highest limit (44.7°), characteristic for many passerine birds. The same level at 50° it reached the body temperature of *C. c. ruficollis* in experience/experiments of J. Harder.

Polypnea (quickenened shallow breathing) begins at the temperature of body 41.5° and of air 30°. At the temperature of body 42.5°, appears heat shortness of breath (panting) - beak is widely opened,

the soft tissues of the lower cavity of mouth and tongue stuck out outside, abundantly are moistened and shake. In ravens thermal shortness of breath begins with the same air temperature (40°), that also in many other birds.

Table 1. Respiration evaporation of water and the percentage of the heat, taken away evaporation, for ravens at rest at the different temperatures of medium.

(1) Показатель	(2) Температура среды, °C					
	10	20	30	36	40	50
Испарение воды, мл/ч (3)	2,0	2,0	3,2	6,0	33,1	45,0
Общая теплопродукция, рассеиваемая испарением, % (4)	13,4	23,0	37,0	68,0	100	120

Key: (1). Indicator. (2). Temperature of medium, °C. (3). Evaporation of water, ml/h. (4). The general thermogenesis, scattered is evaporation, o/o.

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The respiratory (and skin) evaporation of water (Table 1) at 10° takes away 13.4o/o of thermogenesis, but with 20°-23o/o, that noticeably higher than in nonpasserine birds of the same size (King, Farner, 1961). With a further rise in temperature evaporation increases, and at 40° removes 100o/o of the produced heat. At 50° evaporation dissipates 120o/o of the heat production, i.e., heat balance still is preserved. In experience/experiments of J. Marder the *C. c. ruficollis* render/showed capable to scatter 167o/o of thermogenesis. Such high capabilities for cooling evaporation is

unknown in other passerine birds (Kendeigh, 1972).

Energy of existence, expressed in the form of linear dependence on the temperature of medium, takes the form

$$EE = 176 - 0.1 T_A \text{ kcal/day per 1 bird.} \quad (3)$$

If the thermal conductivity of integuments, body temperature, and respiratory cooling by evaporation were invariable/unchanged, metabolism would grow/rise during a change in the temperature of medium in both sides from the point with which side-line thermogenesis from basic physiological processes was equal to a quantity of heat, necessary for maintaining the temperature of body. Of the majority of warm-blooded animals instead of the thermoneutral point, there is a zone of temperatures at which the thermogenesis is constant, and heat balance is preserved because of physical thermostatic control (change in the thermal conductivity of integuments, the temperature of body and the evaporation of water). The wider this zone, the more improved the regulation of heat emission.

The motion of plumage changes heat emission, shortening or increasing the layer of concluded between feathers air. Ptilomotor reaction uses many form/species of passerine birds (Shilov, 1968).

but in this case the thermal conductivity of integuments in small northern birds changes only 1.1-1.4 times (Gavrilov, 1972). Lower boundary of thermoneutrality in this case is displaced in all to 1-3°. The effect of pose must grow/rise in the case of an increase in the length of feathers (with the ruffled plumage the heat-insulating air layer increases) and the decrease in the heat-insulating properties of each feather (with the pressed feathers thermal conductivity is high).

Ravens obtain the vast effect of piliomotor reaction precisely because of such special feature/peculiarities of their plumage. The thermal conductivity of feathers of *C. caurinus* reaches 1.9 kcal/m²·deg·h, i.e., 1.6 times higher than is usual for birds of such dimension (Kendeigh, 1972). The length of the feathers of the raven is well-known; precisely as a result of lengthening of feathers, apparently, the weight of plumage of raven is higher than in the birds of a similar size/dimension. After ruffling plumage, ravens can shorten thermal conductivity 2.67 times. Lower boundary of thermoneutrality is displaced in this case to 16° (from 22 to 6°).

An increase in the temperature of body automatically enlarges the thermoneutral zone to the side of higher temperatures on as many degrees, on as was increased the temperature of body. In the raven this ability is the same as in other passerine birds: at superheating/overheating the temperature rises by 4°. Thus, to the

lot of cooling by the respiratory evaporation of water remains the ten-degree section of vast (from 6 to 36°) thermoneutral zone.

Respiratory evaporation in ravens is developed to a high degree. After all the other adaptations to the preservation/retention/maintaining of heat balance are used, is included thermal shortness of breath, capable of stopping further growth/build-up of thermogenesis and even at 50° preserving heat balance. Adaptation system of the raven proves to be very effective simultaneously, also, for inhabiting under Arctic conditions, and under hot arid conditions.

In recent years were published several generalizing empirical formulas, describing the dependence of the metabolism of sparrow birds on the size/dimensions of body. These formulas reveal/detect the special feature/peculiarities of the organization of detachment and has exceptional value for the understanding of its evolution/maneuver, ecology and bioenergetics.

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In the majority of cases, a dimensional series of the form/species the data on which are used for the calculations of formulas, breaks itself on the form/species of the moderate size/dimensions. After

comparing those obtained by performance calculation for the bird with a weight of 1185 g with experimental data, it is possible to establish/install that the competence/validity of the extrapolation of these formulas to birds, that are found in upper end of the dimensional series, and secondly, the special feature/peculiarity of the metabolism of large passerine birds (Table 2).

Energy of existence of the raven at 30° is higher than is obtained from the formula of Kendeigh, and growth in it less abrupt/steep. The speed of the standard metabolism more follows the formula of Kendeigh than the Lasiewski-Dawson one. But the speed of metabolism at the low temperatures in the formula of Kendeigh is understated: it proves to be less than the standard metabolism. Thermal conductivity in rest for the raven is higher than calculated. The formula, which describes the dependence of respiratory evaporation on size/dimensions, is not suitable for large passerines. The part of these disagreements is explained by an inaccuracy in the formulas, calculated on datum, that cover the restricted number of form/species of passerine birds, moreover only small.

As shown in recent years (Lasiewski, Dawson, 1967; Kendeigh, 1969, 1970, 1972; Dol'nik, 1969), passerine birds have other characteristics of metabolism in comparison with nonpasserine. Differences concern chemical thermostatic control (speed of

thermogenesis which in passerine birds is above). The special feature/peculiarities of the metabolism of passerines are adaptive for the small size/dimensions of body, but are not adaptive for large. Only one group of passerines - the Corvidae - reaches the moderate for nonpasserine birds size/dimensions and it is located in dimensional zone, where the advantages of the metabolism of passerine birds are converted into deficiency/lacks. Nevertheless this group is numerous (104 form/species), are widespread, eurybiontic, and many form/species undoubtedly they flourish. Consequently, Corvidae found a method to remove/take negative consequences of large size/dimensions. On the basis of research on the metabolism of ravens it may be concluded that was achieved/reached this by means of intensifying the physical thermostatic control.

The special feature/peculiarities of the metabolism of passerine birds are led to shift of the large forms of the lower point of thermoneutrality to the side low-temperature.

Table 2. Comparison of some indicators of the metabolism of ravens with the values, calculated for the birds of the same weight (1185 g) by the generalizing formulas for passerine birds.

(1) Показатель	(2) Эксперимент	(3) Расчет по формулам	(4) Литературный источник
Энергия существования, ккал/сутки, при температуре, °C: (5)			
30	143,0	127,5	Kendeigh, 1970
0	176,0	184,6	То же (6)
Теплопроводность при существовании, ккал/град·сутки (7)	1,10	1,90	„ „
Скорость стандартного метаболизма, ккал/сутки (8)	120,0	145,9	Lasiewski, Dawson, 1967, Kendeigh, 1969
Энергия покоя при 0°, ккал/сутки (9)	120,0	117,7	То же (6)
Теплопроводность в покое, ккал/град·сутки	138,2	93,5	Lasiewski e.a., 1967
Респирационные потери воды при 20°, мл/сутки (11)	3,40-6,39	3,18	
	48,0	7,26	Crawford, Lasiewski, 1968

Key: (1). Indicator. (2). Experiment. (3). Calculation according to formulas. (4). Literary source. (5). Energy of existence, kcal/day, at temperature, °C. (6). The same. (7). Thermal conductivity with existence, kcal/deg·day. (8). Speed of standard metabolism, kcal/day. (9). Rest energy at 0°, kcal/day. (10). Thermal conductivity at rest, kcal/deg·day. (11). Respiratory losses of water with 20° ml/day.

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In this case, respectively must be displaced the point with which begins the superheating/overheating, which is nonadaptive. But if it

would be possible not to displace upper boundary of thermoneutrality, expansion of thermoneutral zone would be profitably.

With a gain in weight of body in passerine birds, quantitative characteristics of plumage change in the direction, favorable for lengthening of feathers, since the weight of plumage grow/rises proportional to the weight of body to degree of 1.0 (Turcek, 1966; Kendeigh, 1970), and the number of feathers it increases insignificantly, proportional to the weight of body to degree of 0.18 (Kendeigh, 1970). Consequently, occurs a disproportionate gain in weight of feathers (to degree of 0.82 instead of 0.67) and of their length (to degree of 0.936). Simultaneously feathers become rarer, since body surface increases proportional to the weight of body to degree of 0.667, and the number of feathers only to degree of 0.18). This allows for large birds, changing the position of feathers on body, over wide limits to monitor heat emission and respectively to displace the point of overheating to the side of higher temperatures.

Another adaptation of Corvidae - the intensification of capability for cooling by the respiratory evaporation of water - allowed to preserve upper boundary of thermoneutrality at common for passerine birds level.

These special feature/peculiarities of the metabolism of

Corvidae with the preservation/retention/maintaining by them of the characteristic for all singing birds high level of standard metabolism definitely indicate their origin from small ancestors and the evolutionary youth of group.

The zoological institute of the AN USSR

Submitted on 13 September 1972.

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H300 USAICE (USAREUR)	1		
P005 ERDA	1		
P055 CIA/CRS/ADD/SD	1		
NAVORDSTA (50L)	1		
NASA/KSI	1		
AFIT/LD	1		

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